Taphonomic and ecological insights from conspecific bite marks on *Otodus megalodon* teeth

STEPHEN J. GODFREY, MARK BENNETT, and VICTOR J. PEREZ

Although there is now good representation of shark-bitten bone in the fossil record, shark-bitten shark teeth are still exceedingly rare. A relatively small number of teeth of the Neogene megatooth shark *Otodus megalodon* (Otodontidae) preserve surface markings that were made when struck by the serrated cutting edge of another *O. megalodon* tooth. The serration marks are consistent with those of the ichnotaxon *Knethichnus parallelum*. That these shallowly penetrating surface trace fossils were made as one *O. megalodon* tooth struck another is confirmed by the preservation of fine parallel gouges made when the serrated cutting edge of one tooth impacted and raked the surface of the receiving tooth. The *K. parallelum* marks on *O. megalodon* teeth could have been unintentionally self-inflicted, the result of one tooth striking another in the opposing jaw during forceful occlusion, collateral damage from feeding, or aggressive *O. megalodon*-on-*O. megalodon* facial biting (i.e., either from active predatory cannibalism, a feeding frenzy during scavenging, or as a result of a territorial dispute to establish a feeding hierarchy).

Introduction

There are now many examples of morderolites (Godfrey and Collareta 2022) in the fossil record, including those produced by sharks biting bone and other biogenic materials (Godfrey et al. 2018; Hunt and Lucas 2021; Benites-Palomino et al. 2022; Collareta et al. 2022 and the references therein). These variously named trace fossils document evidence of exploratory behavior, successful or failed active predation, and/or scavenging. However, there are very few published examples of shark-tooth marked shark teeth (e.g., Perez 2020; Collareta et al. 2023).

The extinct Neogene megatooth shark, *Otodus megalodon* (Otodontidae), continues to be a source of endless popular and scientific fascination. This insatiable interest certainly derives from the large size of its serrated teeth and macro-predatory habits. *Otodus megalodon* was one of the largest predators ever, thought to have attained a maximum body length of about 20 m (Perez et al. 2021; Sternes et al. 2024). The anagenetic lineage that culminated in *O. megalodon* evolved during the Cenozoic within a group of lamniform sharks that experienced gigantism both in body and tooth size. During this evolutionary continuum, the megatooth lineage became increasingly specialized at preying upon and scavenging marine mammals (Marx and Uhen 2010; Perez et al. 2019; Pyenson and Koch 2022).

Testament of those trophic encounters is preserved on Cenozoic cetacean bone marked in various ways by *O. megalodon* teeth (Purdy et al. 2001; Renz 2002; Aguilera et al. 2008; Collareta et al. 2017; Godfrey et al. 2018; Mierzwiak and Godfrey 2019). Likewise, geochemical analyses of nitrogen and zinc isotopes derived from tooth enameloid reflect the high trophic position of *Otodus megalodon* as an apex predator (Kast et al. 2022; McCormack et al. 2022).

However, not only were marine mammal bones marked in various ways by the cutting edge of *O. megalodon* teeth, but so were *O. megalodon* teeth. *Otodus megalodon*-bitten *O. megalodon* teeth are, however, exceedingly rare. These marked teeth are usually referred to as "self-bitten" teeth. While *O. megalodon* teeth preserve a variety of bite mark trace fossils (SJG personal observation), here we confine this brief report to those that preserve markings made by the serrations from another *O. megalodon* tooth. Purdy et al. (2001: 135, fig. 41) briefly describe an *O. megalodon*-bitten *O. megalodon* tooth (USNM 326257) that was collected from a spoil pile in the Nutrien Mine (Aurora Phosphate, formerly known as the Lee Creek Mine) in Aurora, North Carolina, USA. Here, we describe four other *O. megalodon* teeth that preserve bite marks characteristic of the ichnotaxon *Knethichnus parallelum* Jacobsen & Bromley, 2009 (Jacobsen and Bromley 2009: fig. 3D). The Purdy et al. (2001) publication predates the naming of this bite mark ichnotaxon (Zonneveld et al. 2022). *Knethichnus parallelum* represents multiple parallel gouges made when the serrated edge of a tooth raked another biogenic surface. *Knethichnus parallelum* are only very rarely found on teeth of any kind (Godfrey et al. 2021).

Institutional abbreviations.—CMM-V, Vertebrate Paleontology Collection at the Calvert Marine Museum, Solomons, USA; USNM Pal, Department of Paleobiology, National Museum of Natural History (formerly U.S. National Museum), Smithsonian Institution, Washington, DC, USA.

Other abbreviations.—a1, a2, lower anterior teeth in file 1 or 2; A1, A2, upper anterior teeth in file 1 or 2; CW, crown width; SCW, summed crown width; TL, total body length.

Material and methods

Four teeth belonging to *Otodus megalodon* and bearing tooth marks are described in this study: CMM-V-13605, 13608, 14606, and 15554. The specimens are housed in the paleontology collection at the Calvert Marine Museum, Solomons, Maryland, USA.

CMM-V-15554 (Fig. 1A), CMM-V-14606 (Fig. 1B), and CMM-V-13605 (Fig. 1C) were collected from spoil piles in the Nutrien Mine in Aurora, North Carolina, USA. The mine is no longer open for the collection of its valuable fossil resources but continues to operate as an active phosphate mine. Although these teeth were not found in situ, experienced collectors recognize the color of these teeth as characteristic of *O. megalodon* teeth originating from within the Pliocene Yorktown Formation. However, we do not know the formational origin of the teeth with absolute certainty, as they might have originated from the Miocene Pungo River Formation.

CMM-V-13608 (Fig. 1D) was collected as float from the bed of the Broad River in South Carolina by scuba diver Matthew "Matty" J. Swilp (Shamokin, Pennsylvania, USA). Although the tooth was not found in situ, from where it was found, it may have originated from within the Middle Miocene Hawthorn Formation. The Middle Miocene diatom assemblage of the Hawthorn Formation is correlative with that of approximately the upper half of Miocene Shattuck Zone 16 of the Choptank Formation (Serravallian) in the Chesapeake Bay region (Maryland, USA) (Abbott and Andrews 1979).

To highlight detail and improve contrast in the figures, the *O. megalodon* teeth were whitened (i.e., very lightly dusted) with sublimed ammonium chloride (a whitening technique described by Cooper (1935) and Feldman (1989)). After the teeth were photographed with a Nikon CoolPix P510 camera under fluorescent light, the ammonium chloride was removed by holding the teeth under running water (Shelburne and Thompson 2016). A freshwater rinse is strongly recommended to ensure that hydrochloric acid does not form from any residual ammonium chloride.

Body length estimates of the bitten *O. megalodon* teeth are based on the summed crown width (SCW) method, using the most complete associated dentition of *O. megalodon* as an analog (Perez et al. 2021). These body length estimates should be taken as an approximation, as the exact tooth positions of the isolated teeth are unknown. Further, Perez et al. (2021) showed that lower tooth positions result in over-estimated body lengths. A body length estimate is not provided for CMM-V-13608 due to the poor preservation and inability to accurately measure the crown width of the tooth. Unfortunately, we cannot provide any body length estimates for the individuals that produced the bite marks.

Results

CMM-V-15554 (Fig. 1A) is 121 mm in perpendicular vertical height and 90 mm across the widest portion of its root. The tooth is very nearly symmetrical about its vertical axis. The slightly concave profile of the serrated edges is characteristic of a lower anterior tooth. The apex of the root, immediately proximal to the bourlette, is marked by approximately 30 closely spaced adjacent gouges. From right to left, the gouges initially course distally over the root at an angle of about 50° to the long axis of the tooth. At a point near the midline of the tooth, the parallel gouges abruptly change direction, initially turning proximally then disappearing off the root perpendicular to the length of the tooth. Based on the SCW method, CMM-V-15554 had a total body length of 16.7–19.5 m (Table 1); however, this is likely an overestimate given that the estimate is derived from a lower tooth position.

Table 1. Estimated body length of the *Otodus megalodon* individuals based on the crown width of each specimen described herein. The abbreviations a1-a2 refer to lower anterior teeth and A1-A2 refer to upper anterior teeth from the first or second tooth file. Abbrevuiations: CW, crown width; SCW, summed crown width; na, not applicable due to damaged specimen; TL, total body length.

Specimen number	Tooth position	CW (mm)	SCW (mm)	TL Estimate (m)
CMM-V-15554	a1-a2	76.3	681.3–794.8	16.7–19.5
CMM-V-14606	A1-A2	84	792.5–884.2	12.5–14.0
CMM-V-13605	a1-a2	50.3	449.1–524.0	11.0–12.8
CMM-V-13608	a1-a2	na	na	na

CMM-V-14606 (Fig. 1B) is 124 mm in perpendicular vertical height and 95 mm across the widest portion of its root. The tooth is very nearly symmetrical about its vertical axis. Its symmetry and gently convex serrated cutting edges in contour are characteristic of upper anterior teeth. On the lingual surface of the tooth just distal to the bourlette, and to the left of its midline, is a small patch of fine parallel gouges (Fig. 1B). The serrated edge of the impacting tooth first struck the receiving tooth diagonally within the bourlette. From that point, the 15 parallel gouges decrease abruptly to only a few as they curve distally along the midline of the tooth. Based on the SCW method, CMM-V-14606 had a total body length of 12.5–14.0 m (Table 1).

CMM-V-13605 (Fig. 1C) was collected by Becky Hyne in Aurora Nutrien Mine. It is 82 mm in perpendicular vertical height and 56 mm across the widest portion of its root lobes. The mesial root lobe is decidedly pointed, whereas the distal root lobe is rounded. In a lingual view of the tooth, the serrated edges are slightly concave, and the shape of the crown is nearly symmetrical, indicative of a lower, right anterior tooth position. The apex of the crown preserves a small spall fracture. Three fine gouges mark the base of the spall, suggesting that it was struck by serrations from the offending tooth. Crossing the base of the enameloid crown on the lingual surface of the tooth, the bourlette, and the distal portion of the root are two diagonal and adjacent serration-gouge slashes (Fig. 1C). The proximal slash is 13 mm in diagonal length and only preserves two faint serration marks that curve distally towards the midline of the tooth. The second more distal cut is 22 mm in length. Descending into this prominent cut line are at least six concentrically curving faint serration gouge marks. The long axis

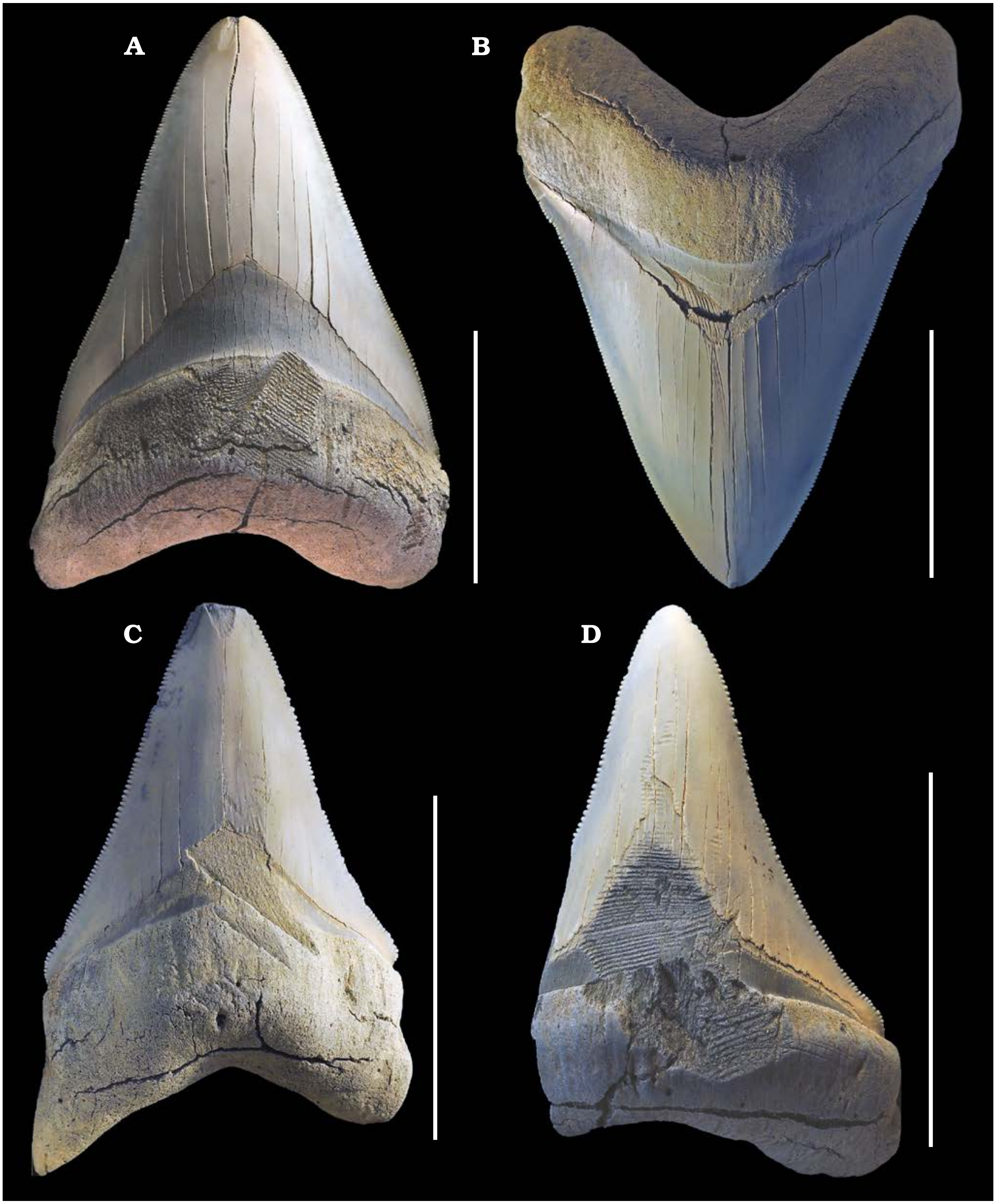

Fig. 1. Teeth of lamniform shark *Otodus megalodon* (Agassiz, 1835) from Aurora, North Carolina, USA, probably Pliocene (A–C) and Broad River, South Carolina, USA, probably Middle Miocene (D), preserving the trace fossil *Knethichnus parallelum* Jacobsen & Bromley, 2009. **A**. CMM-V-15554, a lower anterior tooth in lingual view. These bite marks are preserved in their majority on the apex of the root. **B**. CMM-V-14606, an upper anterior tooth in lingual view. A small patch of fine gouges marks the base of the crown distal and adjacent to the midline of the tooth. **C**. CMM-V-13605, a lower anterior tooth in lingual view. Two areas of bite gouges mark the apex of the root and bourlette respectively. Three fine gouges on the very apex of the tooth suggest that it too was struck by serrations on the opposing tooth. **D**. CMM-V-13608, a lower anterior tooth in lingual view. The bite gouges mark much of the lingual midline surface of the tooth. Teeth lightly whitened with sublimed ammonium chloride. Scale bars 50 mm.

of the serration gouges is subparallel to the length of the tooth. The proximity and parallel orientation of the two cut gouges on CMM-V-13605 suggests that they were made by the same impacting *O. megalodon* tooth. The long axis of the cutting tooth would have been at an angle of about 30° to the long axis of the marked tooth. Based on the SCW method, CMM-V-13605 had a total body length of 11.0–12.8 m (Table 1); however, this is likely an overestimate given that the estimate is derived from a lower tooth position.

CMM-V-13608 (Fig. 1D) is 80 mm in perpendicular vertical height. One of its root lobes was not preserved and therefore the maximum width across the root lobes is unknown. Nevertheless, the tooth is in appearance symmetrical about its vertical axis. Furthermore, the finely serrated cutting edges are both gently concave, characteristic of a lower anterior tooth. A significant portion of the lingual surface of this tooth is marked by serration gouges. In their majority, the striations are preserved either on the root of the tooth or the dentine below the crown of the tooth. A smattering of variously positioned short parallel gouges mark the crown of the tooth. The marks are in two clusters, separated by a small, ragged patch of the broken surface of the root of the tooth proximal to the bourlette. That the serration gouges mark the tooth where both a portion of the root and enameloid surface of the crown are missing suggests that the serrated edge of the marking tooth raked the receiving tooth with sufficient force to spall off those missing surfaces. Most of the gouges cross the lingual face of the tooth essentially perpendicular to its length. Some of the grooves appear to overlap, suggesting that the gouges were made in at least two successive but slightly overlapping passes of the marking serrations over the bitten surface. Due to poor preservation of the root, an accurate crown width measurement cannot be made for CMM-V-13608, preventing implementation of the SCW method to estimate body size.

Concluding remarks

Although there are cases when the maker of a bite-mark trace fossil is unknown, in the *O. megalodon* teeth described here, there is a very high degree of confidence that the *Knethichnus parallelum* traces were made by the serrated cutting edge of other *O. megalodon* teeth. The size and adjacent gouge spacing confirms *O. megalodon* teeth as the origin of the *Knethichnus parallelum* traces. All the teeth described herein (and including USNM Pal 336257, figured by Purdy et al. 2001: fig. 41) were marked on and about the midline of their lingual surface. None of the teeth in our sample were marked with serration marks on their labial surface. However, our sample size is too small to know if this pattern is normative.

We do not know of any posterior *O. megalodon* teeth that preserve *Knethichnus parallelum*. Once again, because the sample size is so small, we are not suggesting with any confidence that anterior teeth are more likely to have been scored.

We do not know under what circumstances any of the *O. megalodon* teeth described herein came to be marked by another *O. megalodon* tooth. One might imagine that the simplest way to account for *O. megalodon*-bitten *O. megalodon* teeth would be that two teeth in opposing jaws struck each other during occlusion, the serrated cutting edge of one marking the other. However, in lamniform sharks, the upper jaw protrudes beyond the lower jaw to such an extent that this would be unlikely (Moss 1977; Wilga 2005). A tooth would have to have been contorted or at least partially out of place for the cutting edge to occlude with and mark the lingual face of an opposing tooth.

Another possibility is that an *O. megalodon* tooth was knocked loose for any number of reasons but remained in the originating jaw of the shark. This shed (or ex situ, but not completely shed) tooth might then have been struck and marked by an in situ occluding tooth. Some extant shark species will ingest their own teeth, possibly unintentionally or as an intentional means of recycling the calcium phosphate (Stransberg 1963; Uchida et al. 1996).

A third possibility is that *O. megalodon* teeth became marked during a predatory or scavenging event. In this scenario, the tooth that would become marked became dislodged in the act of forcefully biting into a prey item. During a subsequent bite, one of its in situ teeth would have serendipitously struck the dislodged tooth with sufficient force to mark it in the process. With the bite force of *O. megalodon* having been estimated to have been between 108,514–182,201 N (more than 10 × greater than the modern great white shark, *Carcharodon carcharias*), there is no doubt that *O. megalodon* possessed sufficient force to produce these bite marks (Wroe et al. 2008). However, since it is not yet known how much force would have been required for one *O. megalodon* tooth to score another, we do not yet know if a shed tooth held in its own jaw, or the compliant flesh of its prey would have remained sufficiently immobile for it to have become marked by the subsequent impact of an in situ *O. megalodon* tooth.

In the final scenario, we envision the possibility of an antagonistic encounter between two *O. megalodon*, perhaps during a territorial dispute to establish a feeding hierarchy, a feeding frenzy, over mating rights, simple aggression, or during the act of cannibalism, either from active predation or scavenging, in which one individual forcefully bit the jaws of its rival (or the carcass of the conspecific being scavenged), marking the receiving tooth as part of that episode. As a possible modern analogue, extant great white sharks (*Carcharodon carcharias*) engage in jaw-to-jaw aggression, possibly brought on during territorial and/or mating disputes, or simple naked aggression. While this behavior is not well documented in the published literature, footage of this behavior has been captured, including in the National Geographic documentary "Cannibal Sharks" (Woodward 2019). Other sharks are known to also engage in acts of cannibalism, and intrauterine cannibalism is common among lamniforms (Gilmore and Dodrill 2005; Shimada et al. 2021).

It is not possible to definitively know the circumstances during which the *O. megalodon*-bitten *O. megalodon* teeth described herein were marked; however, these specimens possibly represent a variety of behaviors worthy of further study regarding the ecology of the largest shark that ever lived.

Acknowledgements.—The scuba diving expertise of Matthew "Matty" Swilp (Shamokin, Pennsylvania, USA) brought one of these remarkable teeth to light. Long-time and passionate avocational collector Becky Hyne recovered another one of the teeth described herein. The other teeth were collected by author (MB). CMM Paleontology Collections Manager John R. Nance is gratefully acknowledged for encouraging access to specimens in his care. We greatly appreciate the valuable input and constructive feedback provided by reviewers Alberto Collareta (Università di Pisa, Italy) and Bretton Kent (University of Maryland, College Park, USA), and the journal editorial team for moving this manuscript through the publication process. Funding for this publication came in part from the citizens of Calvert County Maryland, the County Board of Calvert County Commissioners, the Clarissa and Lincoln Dryden Endowment, and the Duvel-Tuve-Burris Endowment at the Calvert Marine Museum. Were it not for the staff collective at the Calvert Marine Museum, author SJG would not have been able to work on this delightful project.

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Stephen J. Godfrey [Stephen.Godfrey@calvertcountymd.gov; ORCID: https://orcid.org/0000-0002-7916-8791], Maryland Paleontology Collections and Research Center, Calvert Marine Museum, P.O. Box 97, Solomons, Maryland, 20688 USA. Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, 20013-7012 USA. Vertebrate Paleontology, Natural History Museum of Los Angeles, 900 Exposition Boulevard, Los Angeles, California, 90007 USA.

Mark Bennett [PaleoMark@aol.com], Maryland Paleontology Collections and Research Center, Calvert Marine Museum, P.O. Box 97, Solomons, Maryland, 20688 USA.

Victor J. Perez [vjperez@smcm.edu; ORCID: https://orcid.org/0000-0002-0041-7151], St. Mary's College of Maryland, St. Mary's City, Maryland, 20686 USA. Maryland Paleontology Collections and Research Center, Calvert Marine Museum, P.O. Box 97, Solomons, Maryland, 20688 USA.

Received 5 July 2024, accepted 5 November 2024, published online 27 December 2024.